

ON THE ZOÖLOGICAL POSITION OF *PARTULA* AND *ACHATINELLA*.

BY HENRY A. PILSERY, SC.D.

The classification of the land snails has an attraction [for the systematic or morphological malacologist disproportionate to the rank of the group; and once entered upon, the phylogenetic problems presented for solution are surpassed in interest by those of no other group, unless it be the Chitons. The great amount of work along sound lines that has been done since the days of Beck and Held has merely opened the mine, as it were; and the wealth in sight is more abundant than our generation can develop.

In dealing with *Partula* and *Achatinella*¹ it appears that nothing yet written upon their structure and its meaning goes to the root of the matter. Fischer, in his admirable *Manuel*, subordinates *Partula* to *Bulimulus* as a subgenus, and places the family *Achatinellidae* between the *Stenogyridae* and the *Succineidae*. Kobelt² considers *Partula* to be closely allied to *Placostylus*, a genus of the *Bulimulidae*; and others have held a like opinion. Semper grouped *Partula* with *Placostylus*, but in his posthumous appendix on the pulmonate kidney, he recognizes that it has the basommatophorous arrangement of kidney and ureter (p. 70).

It is generally agreed that the primary division of the Stylommatophores into *Monotremata* and *Ditremata*³ is a just one, though the fact expressed in the names has a significance quite secondary to that of the diverse modification of the pallial organs in the two groups.

From the *Monotremata* arose a lateral line, profoundly modified in the structure of the lung, etc., the *Athoracophoridae* or *Janel-*

¹ I have been assisted in the examination of these snails by Mr. E. G. Vanatta.

² *Syst. Conchyl. Cabinet*, edit. 2, *Placostylus*, p. 5, 1891.

³ I used the more expressive term *Teletremata* in my *Catalogue of American Land Shells*, but as stability is better than meaning in nomenclature, the innovation was probably unwise.

lide. Our knowledge of the morphology of this branch is largely due to Dr. Ludwig Plate, who proposes the term *Tracheopulmonata* for the *Janellidae*, the remainder of the monotremate group taking that of *Vasopulmonata*.

The two groups *Ditremata* and *Tracheopulmonata* are strongly specialized, and far from the main line of descent of the mass of the Stylommatophores.

The group of *Vasopulmonata*, comprising a vast majority of the air-breathing snails, has been divided into families by characters of the jaw, teeth, shell, caudal pore, scarcely any two authors agreeing in the number or limits of the families so established. No one can review the classifications given by various authors during the past decade without being impressed by the chaotic condition of the subject. This is largely due to the use of external or peripheral organs in taxonomy; the jaw, teeth, caudal pore and form of the shell being directly acted upon by external conditions or food, consequently changing rapidly, and subject to deceptive convergent development.

The truly primary divisions of the *Vasopulmonata* rest upon the modifications of the pallial region. In one series of forms, of which *Buliminus*, *Partula* and *Achatinella* are prominent members, the ureter passes directly forward from the kidney, toward the anterior margin of the lung. This is also, as is well known, the condition of these organs in the *Basommatophora*, or fresh-water *Pulmonata*, which have been generally, and I believe rightly, considered ancestral to the *Stylommatophora*.⁴ Compare *Partula* (Pl. XVII, fig. 8) and *Limnæa* (Pl. XVII, fig. 2). This direct form of kidney and ureter, together with various other characters, indicates, in my opinion, that *Partula* and its fellows with a direct ureter are members of an ancient and ancestral group lying at the very base of the vasopulmonate phylum. This group I propose to call *Orthurethra*.

In all the other groups of *Vasopulmonata* the position of the ureter relative to other pallial organs has been changed, though least in the *Succineidae* and certain macroögonous genera. From the apex of the kidney the ureter is abruptly reflexed, passing to the posterior end of the lung-cavity. Thence an open groove or

⁴ Compare Semper, *Reisen im Archip. Phil.*, III, zweites Ergänzungsheft, p. 70.

a closed tube continues across to the last fold of the gut, which it follows forward to the mantle-edge. This continuation of the ureter is morphologically merely a narrow strip of the ærating surface of the lung set apart by a slight ridge to form a canal, or, in more advanced forms, a tube. It has been aptly called the "secondary ureter," or the gut ureter—*Darmharnleiter* of German anatomists. The snails having this sigmoid form of ureter (Pl. XVII, fig. 6) I propose to segregate as a group, *Sigmurethra*, taxonomically standing equal in rank to its parent group, the *Orthurethra*. The open or closed condition of the secondary ureter is a matter of very little importance. The backward flexure of the primary or true ureter is the significant character, indicating as it does a total change in the route by which the "urine" is conducted from the system.

The group *Orthurethra* consists, so far as I know, of some four or five families, not separated by characters of great importance. The *Sigmurethra*, on the other hand, contains numerous family groups of very unequal relationships *inter se*. The further division of the group is based upon characters of the foot, lung, central nervous system, radula, etc.,⁵ the main outlines or skeleton of the system being about as follows:

- I. Margin of the foot defined by grooves, etc., . . . AULACOPODA.
- II. No pedal grooves.
 - A. None of the teeth of the aculeate or thorn-like type; jaw present, distinct, HOLOPODA.
 - B. All of the teeth aculeate, thorn-shaped; jaw often obsolete. Carnivorous.
 - α. Cerebral ganglia concentrated, in close contact, AGNATHOMORPHA.
 - β. Cerebral ganglia separated, a rather long commissure connecting them, AGNATHA.

⁵ Full discussion of the divisions of *Sigmurethra* is not practicable in this place as it will require extensive illustration. Moreover, material in some families is still eluding me. I have therefore not attempted a partial treatment, but merely give a synopsis of results.

The system of *Vasopulmonata* may then be roughly tabulated thus :

Vasopulmonata.	{	Orthurethra.	{	Subdivisions, if any, to be de- termined.	Partulidæ.
					Pupidæ.
	{	Heterurethra.	Elasmognatha.	? Valloniidæ.	
				? Cochlicopidæ.	
	{			Achatinellidæ.	
				Succineidæ.	
	{		Holopoda.	Acavidæ.	
				Helicidæ.	
	{			Bulimulidæ.	
				Urocoptidæ.	
	{			Clausiliidæ.	
				Achatinidæ.	
	{		Agnathomorpha.	Glandinidæ.	
				Rhytididæ.	
	{		Agnatha.	Streptaxidæ.	
Circinariidæ.					
{	Sigmurethra.		Testacellidæ.		
			Zonitidæ.		
{		Aulacopoda.	Limacidæ.		
			Endodontidæ.		
{			Arionidæ.		
			Philomycidæ.		

Probably there are some other groups of family value, though, of course, no anatomist could multiply families with the liberal hand of some recent writers.

The family *Acavidæ* is here understood to be equivalent to the *Acavine* of my arrangement of Helices, with the addition of *Strophocheilus*, which forms a remarkable and archaic subfamily. The *Helicidæ* is not the group so called by Fischer, but stands as defined in *Man. Conch.* (2), ix, minus the Macroögonæ. *Circinariidæ* is a new name for *Selenitidæ*, *Selenites* being preoccupied. I have elsewhere discussed the families of *Aulacopoda*. The *Urocoptidæ* (*Cylindrellidæ*) and *Pupidæ* have been sadly mixed by Fischer; the former family has been the subject of a paper by Mr. Vanatta and myself.⁶ Other families need no special remark.

The foregoing is sufficient to show the general position in the system of *Achatinella* and *Partula*, which may now be considered in more detail. What follows is the joint work of Mr. E. G. Vanatta and myself.

Partula rosea Brod.

The specimens dissected were collected by Andrew Garrett.

Pallial organs (Pl. XVII, fig. 8).—The pulmonary vein is the

⁶ *Proc. Acad. Nat. Sci. Phila.*, 1898, p. 264.

only blood-vessel visible on the lung wall, the general surface being smooth, densely peppered with white specks in parallel lines; the heart is placed obliquely against the kidney (fig. 8, *k.*), which is short and triangular. From the apex of the kidney arises the ureter (fig. 8, *u.*), which runs directly forward, opening by a lateral pore at its end, which is remote from the mantle edge.

Digestive system.—The jaw and teeth have been described by Binney and others. There is a fusiform crop and moderately dilated stomach (fig. 8).

Genitalia (Pl. XVII, fig. 1).—The penis is quite stout with terminal retractor, and divided internally into a lower, coarsely wrinkled portion and an upper densely granulose and coarsely plicate portion. The vas deferens opens above a papilla at about the lower third of the granulose part. The vas deferens is bound to the penis, to the vagina and basal portion of the spermatheca (the adnate portion being shown by dotted lines in fig. 1); it is then free as far as the upper portion of the oviduct, where it is again shortly adnate. The ovisperm duct is strongly knotted as usual.

The basal portion or duct of the spermatheca is much swollen, the upper part being conspicuously smaller and tapering. There is an egg in the oviduct in the preparation figured.

Free muscles (Pl. XVII, fig. 4).—The buccal retractor is free to its proximal insertion. At about the middle of its length the left ocular and tentacular retractor joins it, and a little further out the anterior foot retractors branch off. The broad posterior pedal or tail retractor is united far forward with the right ocular and tentacular retractor, which gives off a group of anterior pedal retractors (fig. 4). The right ocular retractor passes between ♂ and ♀ branches of the genitalia.

This muscle system differs from that of *Achatinella* chiefly in the union of the right ocular retractor with the tail retractor. In the latter genus both ocular retractors are free.

Achatinella dolei Baldwin.

The specimens dissected were received from Mr. D. D. Baldwin.

Pallial organs (Pl. XVII, fig. 3).—The broad pulmonary vein is the only conspicuous blood-vessel. The surface of the lung is heavily pigmented and intensely black, except anteriorly near the rectum, where it is paler. It is traversed by very fine veins transverse to the pulmonary vein. The heart lies parallel with the

kidney. The anterior end of the pericardium and the adjacent surface of the kidney are blotched and dotted with black pigment. The kidney is bulbous or ovate, passing into a wide, pale-colored ureter, which runs directly forward nearly to the anterior edge of the mantle. From its apex a narrow ridge or thread runs backward a short distance on the side toward the rectum; the space between this thread and the ureter having the pigment arranged in oblique striæ.

Digestive system (Pl. XVII, fig. 3).—The jaw and teeth of *Achati-nella* have frequently been figured, and need not be described here. The salivary glands (*s.g.* and fig. 3*a*) are united above and below the œsophagus, forming a complete ring. The œsophagus is long and unusually slender, not dilated into a crop. The stomach is much lengthened, curved at the end. Intestine unusually long, especially the fourth fold (fig. 3, on the right side).

Genitalia (Pl. XVII, fig. 7).—The external orifice is on the left side, as usual in sinistral species. The penis is moderate in length, cylindrical, with terminal retractor muscle and vas deferens. From the middle of its length arises a very long, vermiform appendix (*ap.*), which is irregularly coiled, and between the lower third and fourth of its length is conspicuously constricted for a short distance. Near the base of the appendix a branch of the retractor muscle is inserted, passing to the apex of the penis. The lumen of the penis is narrowed above by two large pilasters, at the apical end of which the vas deferens enters. The orifice communicating with the cavity of the appendix is situated at the lower end of one of the pilasters.

The vas deferens is completely free from the other organs, from its lower insertion to the base of the albumen gland, where it becomes adnate.

The vagina is quite short. The spermatheca is small and ovate, upon a very long, slender duct, and is imbedded in the albumen gland (but shown removed therefrom in the figure). There is a long free oviduct, and a sacculated uterus, much distended by the young contained in the individual figured. The albumen gland is divided into slender cæca (fig. 7*a*), clustered in a dense mass.

Free muscles (Pl. XVII, fig. 5).—The retractor muscles of the tentacles are free from the tail retractor, and both divide into three branches, ocular, tentacular and anterior pedal, at about the mid-

dle of their length. The left ocular band passes between ♂ and ♀ branches of the genitalia. The buccal retractor (*ph.r.*) unites with the left tentacular band at about the posterior fourth of the latter; it is deeply bifurcate anteriorly. The retractor of the tail (*t.r.*) is normal except in its freedom from both tentacular bands.

While *Achatinella* is obviously allied to *Partula* by the direct ureter and plain aerating surface of the lung, it differs so conspicuously in other characters that no very close relationship can be admitted. The ureter in *Achatinella* approaches nearer to the anterior edge of the mantle, and has a terminal ridge, apparently homologous with that of *Limnæa*. The digestive system is lengthened, though of the ordinary four-folded type. The genital system approaches that of *Buliminus* in the appendix of the penis, but is peculiar in the freedom of the vas deferens from the oviduct. In this peculiarity, however, *Partula* shares to a great extent, the adhesions being superficial. The unique structure of the albumen gland and its envelopment of the spermatheca are more aberrant characters. Usually a long-stalked spermatheca is caught with the gut by the cephalic branch of the aorta, and lies near the heart, separated from the albumen gland.

The family *Achatinellide* is apparently a group of great antiquity, the archaic pallial organs and male genitalia being associated with peculiarly specialized female reproductive organs.

EXPLANATION OF PLATE XVII.

- Fig. 1. *Partula rosea*. Genitalia.
 Fig. 2. *Limnæa stagnalis*. Pallial region and digestive tract.
 Fig. 3. *Achatinella dolei*. Pallial region and digestive tract.
 Fig. 3a. *Achatinella dolei*. Lateral view of salivary gland.
 Fig. 4. *Partula rosea*. Free retractor muscles, dorsal aspect.
 Fig. 5. *Achatinella dolei*. Free retractor muscles, dorsal aspect.
 Fig. 6. *Rumina decollata*. Pallial region and digestive tract.
 Fig. 7. *Achatinella dolei*. Genitalia.
 Fig. 7a. *Achatinella dolei*. More enlarged tubules of the albumen gland.
 Fig. 8. *Partula rosea*. Pallial region
ap., appendix; *k.*, kidney; *l.o.r.*, left ocular retractor;
l.t.r., left tentacular retractor; *ph.*, pharynx; *s.g.*, salivary gland; *sp.*, spermatheca; *s.u.*, secondary ureter;
t.r., tail retractor; *u.*, ureter.